

## Circadian Rhythm of Locomotor Activity in a Teleost, *Silurus asotus*

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**ABSTRACT**—Circadian locomotor activities were examined in the nocturnal catfish, *Silurus asotus*. Under constant darkness (DD), the overt rhythm of locomotor activity lasted, in most cases, for 5–10 days, then disappeared. The ratio of fish with circadian activity under DD was higher (approximately 94%) than those under the other experimental conditions described below. Persistence of circadian activity for 5–10 days and subsequent arrhythmicity were also found under constant light (LL).  $\tau$  value and total amount of locomotor activity tended to decrease with an increase in light intensity. Under the condition of dark pulses (DP), the circadian activity was observed but not prominent as those in DD. The participation of intrinsic rhythmicity on diel locomotor activity was examined by delaying and advancing the LD phases. Resynchronization to the new LD cycle was attained within 1–2 days. In conclusion, the data suggest that, despite the high ratio of fish with intrinsic rhythmicity of locomotor activity, the timing mechanism for diel locomotor activity is fundamentally dependent on the external LD cycles.

### INTRODUCTION

Although the circadian rhythm of locomotor activity is well established in mammals [1], birds [2] and reptiles [3], it is not fully documented and still controversial in fish. The existence of circadian rhythm in fish has been demonstrated under constant light and darkness [4–13], whereas other fish display arrhythmicity [14–17].

The persistence of circadian locomotor activity in many fish under constant conditions is relatively low compared with that in higher vertebrates. Overt rhythm of locomotor activities in some fish disappears within several days after imposition of constant conditions [18–21]. Moreover, inter- and/or intra-individual variability has also been demonstrated [21–23].

In order to gain a better understanding of the circadian system of the catfish, *Silurus asotus*, the following experiments were performed. The rhythmicity of circadian locomotor activity was

measured under three different conditions; constant darkness (DD), constant light (LL) and dark pulses (DP). The circadian rule [24, 25] was tested by measuring period length ( $\tau$ ) and total amount of activity under different intensities of constant light. The participation of intrinsic rhythmicity on the diel locomotor activity was examined by shifting the LD phase.

### MATERIALS AND METHODS

Catfish of 21–33 cm in total length and 90–215 gm in body weight were used. They were caught in local rivers of Aichi prefecture during May to October in 1985–1987 and kept in laboratory tank. All fish were placed in an acclimatized tank under 12 hr light and 12 hr dark (LD12:12, L=100 lx, D=complete darkness) at 20°C before the experiments.

Fluorescent light (regulatory fluorescent lamp, National, NQ-21550) was set above the tank as the light source for the L phase of the light regime of LD12:12. A heat absorbing filter was placed in front of the light source. Light intensity was

adjusted with neutral density filters (Lee filters). Attenuation by a filter was 1 log unit. The light intensity without neutral density filters, measured at the water surface of the experimental tank, was adjusted to 100 lx.

Measurement for locomotor activity was carried out on individual catfish in a tank ( $30 \times 30 \times 45$  cm) of which the aerated water depth was 10 cm. The tank was placed in a light proof chamber. All experiments were performed at water temperature of 20°C. Locomotor activity was detected by an infrared sensor (Omron, E3D-10M2) set at both sides of the tank. When the fish swims in front of the sensor, the interruption of the infrared light beam was recorded as one count. The shallow water depth was employed to minimize activities outside the infrared light beam (3-5 cm in diameter). Count numbers exceeding 4/sec were cancelled because high frequency counts might be caused by tail beats or small, incomplete intersections of the light beam. Activities were recorded for more than 17 days. Catfish were randomly fed live 1-2 goldfishes once a day, but not fed under constant conditions. All data were recorded by an event recorder (Shinwa Riken, SAC-10P). Simultaneously, counted numbers for each hr were stored in a microcomputer (NEC, PC-8801).

At the end of the experiment, data were converted to periodogram for each animal. Period lengths of the recorded locomotor activity and their statistical significance relative to random "noise" in the time-series data records were determined by the periodogram [26]. In the present study, circadian activity was determined by 95% confidence limit.

#### *Experiment 1. Circadian rhythm of locomotor activity under constant darkness (DD)*

This experiment was designed to determine whether a catfish has endogenous locomotor activity under DD condition. Sixteen intact animals were used in this experiment. They were exposed for at least a week to LD12:12 ( $L=100$  lx,  $D=$  complete darkness) during the period of entrainment. After the entraining period, locomotor activity of individual fish was recorded under DD for 10-22 consecutive days.

#### *Experiment 2. Circadian rhythm of locomotor activity under constant light (LL)*

The purpose of this experiment was to investigate the intrinsic locomotor activity under LL condition. In addition, it was designed to test the so-called circadian rule with respect to the period length of free-running ( $\tau$ ) and the total amount of locomotor activity (mean count/day) [24, 25]. Thirty-two fish were used in this experiment. Entraining conditions to the LD cycle were the same as experiment 1.

Locomotor activities were measured under 4 different intensities of light; 0.01, 0.1, 1 and 10 lx. To exclude after-effects [27, 28], all experimental animals were pre-exposed to the same LD cycle ( $L=100$  lx,  $D=$  complete darkness) for one week before exposure to each of the 4 LL intensities. After entrainment, fish were exposed to constant light for 10-22 days. To test the circadian rule on the relationship between  $\tau$  and light intensity a completely randomized design was employed. Four groups of fish (6 fish each), each exposed to 1 of 4 given LL intensities, were used for the analysis. Each fish represents 1 replication. To examine the relationship between total locomotor activity and light intensity, the data from fish that mentioned above were used for analysis. The animals were divided into 4 groups (6 fish each), each corresponding to a given light intensity. Each fish represents 1 replication. The locomotor activity was measured for 5 days and averaged. The results were analyzed by the paired t-test.

#### *Experiment 3. Circadian rhythm of locomotor activity under repeated dark pulses (DP)*

This experiment was designed to observe the effect of dark pulses (DP) on locomotor activity. Dark pulses are thought to enhance free-running rhythmicity and reduce the rapid disassociation of the multi-oscillatory circadian system in some fish [20]. Dark pulses were composed of 15 min of complete darkness alternating with 45 min light ( $L=100$  lx) (LD 0.75:0.25). The experimental period lasted for 10-22 days. Eight fish were used in this experiment. Entraining conditions before exposure to dark pulses were the same as those in experiment 1.

#### Experiment 4. Shifting of the LD phase

Shifting the LD cycle was employed to examine the contribution of endogenous mechanisms on diel locomotor activity. The initial light phase started at 6:00 and ended at 18:00. The LD cycles continued for at least a week. Then the LD cycle was delayed for 6 hrs by lengthening the dark phase 6 hrs and changing the time of light-on and -off to 12:00 and 24:00, respectively. After the phase shift of the LD cycle, locomotor activity of the fish was recorded for another 9 days. Then, the LD cycle was advanced 6 hrs by shortening dark phase 6 hrs returning the light-on and -off times to 6:00 and 18:00 again. Then, locomotor activity was recorded for another 8 days. Two different intensities (0.1, 100 lx) for the light phase were used in the shifting experiment. This experiment was performed using 7 fish.

## RESULTS

#### Experiment 1. Circadian rhythm of locomotor activity under DD

All fish showed active behavior in the dark when they were subjected to the LD cycles. The catfish displayed continuous activity mostly after the offset of light which ended after the onset of light. With imposition of constant darkness, the animal lost synchrony with the previous LD cycle and freeran as shown in Figure 1. Most catfish showed overt circadian rhythmicity for 5–10 days as shown in this fish. Although instability of free-running activity may be a common feature in catfish, it was lasted for, in a few cases, more than 20 days. The persistence of circadian rhythmicity of catfish was longer when compared with other species of fish.

$\tau$  values, measured in a total of 15 animals by periodogram analysis in which transient cycles were excluded, were between 22.5 and 27.3 hr ( $24.64 \pm 0.38$  hr, mean  $\pm$  SEM). The occurrence ratio of fish with circadian rhythmicity under the DD was approximately 94% (15/16).

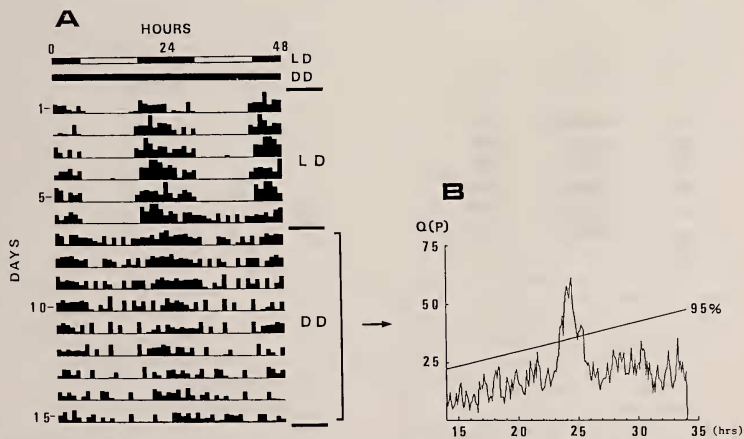


FIG. 1. A record of locomotor activity in a catfish kept under LD 12:12 (100:0 lx) and constant darkness (DD). White and dark bars at the top of the panel represent L and D phases. B. Periodogram derived from analysis of the actogram under constant darkness (DD). The Q(p) values in the periodogram above the 95% confidence limit (slanted line) are significantly different from random noise. The record was double plotted for clarity.

### Experiment 2. Circadian rhythm of locomotor activity under LL

A total of 32 intact catfish was used in the LL experiments, using 4 different intensities of white light. As shown in an example record in Figure 2, rhythmicity of locomotor activity was detected when animals were subjected to LL ( $L=10$  lx). The circadian rhythm in the actograms seemed less clear in LL compared to those in DD. The ratio of fish with circadian rhythmicity for all light intensities was approximately 75%. Overall  $\tau$  values were between 20.1 to 27.0 hr. The values were calculated from data collected for 5–10 days in which transient cycles were excluded.

The relationship between light intensity in LL and  $\tau$  value is shown in Figure 3. The dependence of  $\tau$  on intensity was demonstrated. Although a pair of  $\tau$  values between 0.1 and 1 lx was insignificant, those of the other pairs (0.01 and 0.1 lx, 1 and 10 lx) were significantly different ( $p < 0.001$ ,  $p < 0.05$ ). The data suggest that the correlation of  $\tau$  and light intensity is negative.

The relation between different light intensities

and mean locomotor activity is shown in Figure 4. It was observed that only a pair of results between 0.01 and 10 lx was significantly different ( $p < 0.01$ ). However, there was a tendency that mean locomotor activity decreased with an increase of light intensity.

### Experiment 3. Circadian locomotor activity under DP

The circadian locomotor activity was detected under DP, but not prominent as those in DD. As shown in Figure 5, circadian activity was not clear by visual inspection of this actogram but it was detected by the periodogram. Six out of eight animals showed circadian rhythmicity under the condition of dark pulses. The total  $\tau$  values, which were analyzed without transient cycle, were between 20.9 and 27.5 hr ( $24.71 \pm 1.07$  hr, mean  $\pm$  SEM).

### Experiment 4. Shifting the LD phase

As described above all fish showed typical active behavior in the dark under the LD cycles. After the LD cycle was delayed 6 hr at day 10 (Fig. 6),

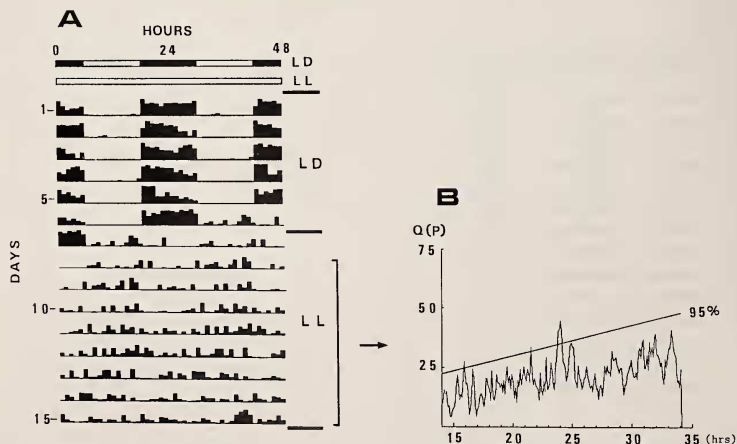


Fig. 2. A. An example of locomotor activity in a catfish held under LD 12:12 (100:0 lx) and constant light (LL,  $L=10$  lx). B. Periodogram derived from analysis of the actogram under constant light. Other features are as described in Fig. 1.

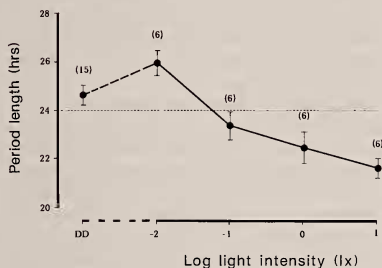


FIG. 3. Relationship between mean free-running period ( $\tau$ ) during 5–10 days and intensity of continuous illumination (lx) in catfish. Closed circles represent the  $\tau$  means and vertical lines indicate the SEM. Numbers in parentheses indicate the number of fish used. Values for DD were derived from experiment 1.

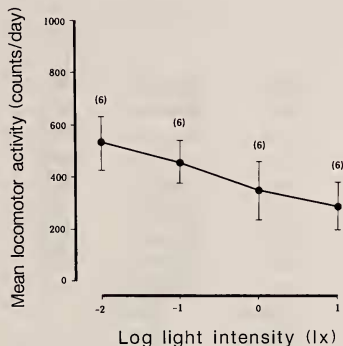


FIG. 4. Relationship between mean amount of locomotor activity and intensity of continuous illumination (lx) in catfish. Closed circles indicate the mean locomotor activity and vertical lines represent the SEM. Numbers in parenthesis indicate the number of fish used.

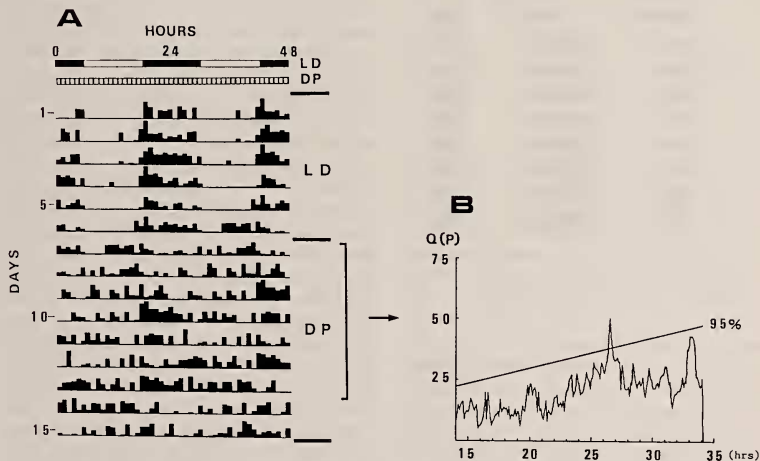


FIG. 5. An example of locomotor activity of a catfish kept under LD 12:12 (100 lx), then exposed to dark pulses (LD 0.75:0.25, L=100 and D=0 lx). B. Periodogram derived from analysis of the actogram under dark pulses. Other features are as described in Fig. 1.

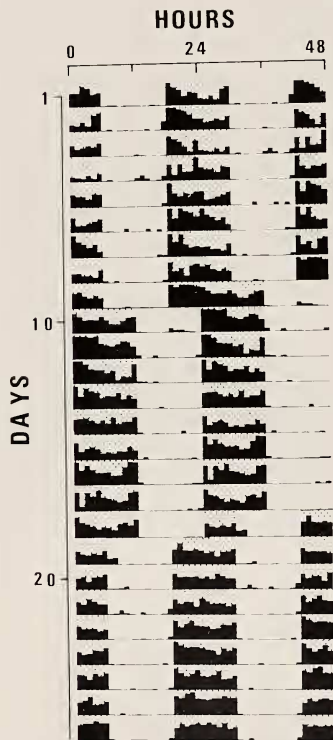


FIG. 6. Double plot of locomotor activity of a catfish in response to a phase shift of LD 12:12 (L=100 lx). Shaded areas indicate the D phase.

the animal displayed locomotor activity during the prolonged dark phase. Small amount of activities were observed during the initial day of the newly changed light phase comparable to that during the period corresponding to the previous dark phase. However, a stable nocturnal pattern was quickly achieved. Resynchronized activities to the phase shifted LD cycles were observed afterwards. After 8 days, the LD cycle was shifted again by advancing the LD regime 6 hr. After the phase shift some

locomotor activity was observed during the new light phase on the first day. Locomotor activity ceased after a few hrs. However, the activity was completely synchronized to the new LD cycles for the subsequent days.

The same protocol was conducted using a different light intensity during the L phase (0.1 lx). As shown in Figure 6, all actograms revealed a similar pattern of behavior indicating small amounts of transient activity during the light phase immediately after changing the LD regime.

The requirement of resynchronization to the new LD cycles was 1-2 days in the shifting experiments under the intensity of both 0.1 and 100 lx. The same period of transient cycles following the delay and advance of the LD phase (symmetry-effects) were apparent.

## DISCUSSION

Despite the fact that endogenous locomotor activity is prolonged, lasting for 100-300 cycles in some higher vertebrates [29, 30], instability of free-running activity is commonly observed in many species of fish. The circadian activity pattern in fish is labile and fades-out easily. Moreover, intra- and inter-individual variations in activity rhythms appears to be common in fish [21-23]. Although the ratio of fish with circadian rhythmicity under constant conditions was higher in catfish than in other species of fish [4-13], similar characteristics of instability of the circadian rhythm of locomotor activity reported in many other fish were observed. One of the reasons for the unstable nature of the rhythm in fish is thought to be the multiple components of the locomotor activity system [31, 32]. In contrast to fish, only a single criterion of behavior is observed in the circadian or entrained activity in higher vertebrates [33]. It has been documented that, under LL conditions,  $\tau$  depends on the intensity of light. According to the so-called Aschoff's rule [24, 25], termed by Pittendrigh [27],  $\tau$  decreases but total amount of activity increases with increased intensities in light active animals, whereas the relationship is reversed in night active animals. According to this rule the definition for teleosts has been contradicted. Electric fish, *Gymnorhamphichthys hypostomus* [34],



killifish, *Fundulus heteroclitus* [7], cyprinid, *Leucaspis delineatus* [35], and diurnal juvenile pink salmon, *Onchorhynchus gorbuscha* [21] obey this rule, but not the lake chub, *Couesius plumbeus* [31] or nocturnal juvenile pink salmon [21]. There are also several other exceptions to this rule in other species of animals [36]. Instead of grouping data from nocturnal and diurnal animals for analysis, Pittendrigh and Daan [37], proposed that  $\tau$  is lengthened in LL with increasing light intensity in species with  $\tau_{DD} < 24$  hr, while it is shortened in species with  $\tau_{DD} > 24$  hr (cf. [36]). In a strict sense, the results obtained in the present experiment do not obey Aschoff's rule, but fit the modified Aschoff's rule with respect to  $\tau$  and total amount of activity.

Arrhythmicity or extinction of a rhythm occurs in many fish when they are kept under constant conditions. These characteristics of circadian activity are thought to be associated with a multi-oscillator system in some species of fish. The circadian system of these fish is considered to be composed of two or more groups of loosely coupled oscillators synchronized to dawn and dusk [22, 38–40]. If a fish is kept under constant conditions, the oscillators are uncoupled, resulting in free-run with their own periods of activity. This could cause arrhythmicity or disappearance of circadian rhythms. If disassociation of the loosely coupled oscillators could be prevented in some way, intrinsic activity might appear in fish. Based on this hypothesis, Eriksson & van Veen [20] applied a light and dark regime of LD 0.75:0.25 instead of LL or DD. This procedure stabilized and prolonged the free-running rhythm in the brown bullhead. However, in our experiment, a 15 min dark pulse every hour did not stabilize or prolong circadian activity. Rather, it caused an opposite effect on locomotor activity of the catfish. The frequency of circadian activity under the dark pulses decreased compared to that of DD. This indicates that (1) dark pulsing causes a dissociation of the oscillators that control circadian activity or (2) possible existence of a circadian organization in catfish differing from a multi-oscillator system.

LD cycle is an effective entraining agent in many species of fish, resulting in diurnal, nocturnal and/or crepuscular patterns of behavior. The endoge-

nous nature of these diel locomotor activities, however, has not been characterized well. When endogenous factors are strongly associated with the timing mechanism under LD condition, delaying or advancing the LD regime causes the appearance of several transient cycles. Duration of transient period is known to depend on the direction of the LD shift. It is generally shorter for delay-shift compared to advance-shift. If several days are required for an animal to synchronize to a new LD cycle, the timing mechanism of locomotor activity has an endogenous component [24, 41]. On the other hand, if an animal synchronizes to a new LD cycle within a day, activities may be exogenously controlled [2, 24, 41]. The endogenous control in fish, examined by shifting the LD regime, has been shown in hagfish, *Eptatretus burgeri* [11], swell shark, *Cephaloscyllium ventriosum* [5], and river chub, *Zacco temminckii* (Tabata and Minh-Nyo, unpublished). On the other hand, exogenous control of locomotor activities has been demonstrated in horn shark, *Heterodontus francisci* [5], juvenile pink salmon, [21], juvenile American shad, *Alosa sapidissima* [15], Atlantic salmon parr, *Salmo salar* [42] and Ayu, *Plecoglossus altivelis* (Tabata and Minh-Nyo, unpublished). In the present study, resynchronization to a new LD cycle following a shift in either direction was attained after 1–2 transient cycles. This was observed with both intensities of light (0.1 and 100 lx). The weaker intensity used in the present experiment (0.1 lx) is strong enough to be sensed by the lateral eye and the pineal organ but is not an effective stimulus for the extraretinal and nonpineal photoreceptors which are associated with the 24 hr locomotor activity of catfish [43]. Hence, despite the high ratio of fish with circadian activity observed under both constant light and darkness conditions, it is suggested that the timing mechanism for diel locomotor activity of the catfish is, fundamentally, based on external LD cycles perceived by the lateral eyes and the pineal organ.

Parametric and nonparametric effects may be mediated by different photoreceptors as described by Underwood and Menaker [44]. Catfish possess three or more photoreceptors which are involved in eliciting locomotor activity and entrainment [43,

45]. Moreover, the contribution of photoreceptors to photoreception is also species-dependent (Tabata *et al.*, unpublished). Additional studies are needed to determine whether differences in receptor mechanisms are responsible for the  $\tau$  values observed under different light intensities of constant illumination.

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